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INDICATORS OF RED SQUIRREL (*TAMIASCIURUS HUDSONICUS*) ABUNDANCE IN THE WHITEBARK PINE ZONE

David J. Mattson[1] and Daniel P. Reinhart[2]

ABSTRACT.—We investigated occupied squirrel middens and squirrel sightings and vocalizations as indicators of red squirrel (*Tamiasciurus hudsonicus*) abundance in the high-elevation whitebark pine (*Pinus albicaulis*) zone. Data were collected 1984–1989 from line transects located on 2 study sites in the Yellowstone ecosystem. We evaluated the performance of each measure on the basis of precision and biological considerations. We concluded that, of the 3 measures, active middens were the best indicator of red squirrel abundance. We also observed that the density of active middens dropped by 48%–66% between 1987 and 1989, following a severe drought and extensive wildfires that burned one of the study sites during 1988.

Key words: transect, Fourier series, midden, vocalization, sighting, wildfire.

Whitebark pine (*Pinus albicaulis*) seeds are an important bear food that affects the survival and fecundity of grizzly bears (*Ursus arctos*) in the Yellowstone ecosystem. Use of pine seeds by grizzlies is almost entirely contingent upon the availability of cones cached in middens (i.e., larder hoards) by red squirrels (*Tamiasciurus hudsonicus*). Management of whitebark pine habitats for grizzlies has thus become contingent upon management of red squirrel populations (Mattson and Reinhart 1994).

We studied red squirrels in the whitebark pine zone using data collected from line transects. Because these data included counts of middens, animals, and vocalizations, we were able to evaluate the relative efficacy of these 3 indicators of squirrel presence. We were interested in identifying a "well-behaved" and relevant indicator of density to facilitate our investigation of relationships between squirrel abundance and environmental factors such as midden use by grizzly bears. We were also interested in providing managers with an approach they could use to indicate squirrel abundance, short of using intensive methods that relied upon marked animals.

STUDY AREA

Our study area consisted of 2 sites, one located on the Mt. Washburn massif in north central Yellowstone National Park (44°47′N), and the other near Cooke City, Montana, immediately northeast of the park (45°00′N). These sites spanned the whitebark pine zone, from 2360 to 2870 m elevation. The whitebark pine zone borders upper timberline and is accordingly cold (average annual temperatures <0°C), often windy, and subject to deep (1–2 m) winter snow accumulations (Weaver 1990).

MATERIALS AND METHODS

Broad study objectives affected our transect design. We mapped the study area by habitat type-cover type strata based upon ground-truthed interpretation of 1:20,000 aerial photography. The result was a fine-scale mosaic, with individual map polygons (forest stands) sometimes as small as individual squirrel territories. To minimize effects of edge between different habitat types, we placed transects so as to maximize the number of right-angle intersections with stand boundaries as well as the amount of intersection with stand interiors. Because of this consideration and because forest and meadow were variously intermixed, transect lines were of unequal length.

We surveyed transects in the same order each year, beginning after 10 August and ending prior to 28 September. Two observers walked permanently marked transect lines, with one observer primarily responsible for observations and the other primarily responsible for recording

[1]National Biological Service, Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83843.
[2]U.S. National Park Service, Resource Management, Yellowstone National Park, WY 82190.

data and keeping on line. At least one of the observers (the junior author) was the same during all years at both sites. Vocalizations and observed squirrels or middens (both active and inactive, by criteria of Finley [1969]) were recorded along with their estimated perpendicular distances from the transect line. Individual cone caches were not considered to be a "midden" and were easily distinguished from these larger, more permanent features.

We used the computer program TRANSECT (Burnham et al. 1980) to estimate densities. Individual transects constituted sample units for density calculations. As recommended by Burnham et al. (1980), we used the Fourier series, with 1–4 terms, to estimate distance-to-line probability detection functions (g[x]). The distance at which we specified the limits of detectability for our measures (i.e., the cut-point) exerted considerable influence on the fit of the Fourier function to the observed detection distribution. Accordingly, we varied cut-points to achieve the best fit to each year- or site-specific data set. Because data were collected from only 35 transects on the Mt. Washburn massif during 1984 and from 15 transects in the Cooke City area during 1984 and 1989 (compared to 57 and 21 transects, respectively, for all other years), we also calculated densities solely from these original 35 and 15 transects for all years so as to allow comparison with results from 1984.

RESULTS

We sampled the study area 5 yr, 1984–1987 and 1989. During 1988 wildfires burned 562,000 ha of the Yellowstone area, including 52% of the Mt. Washburn transects (47% severely). Transects on the Mt. Washburn area totaled 18.9 km during 1984 (mean transect length [$\bar{X}$] = 539 ± 245 m [*s*]) and 29.8 km during the remaining 4 yr ($\bar{X}$ = 523 ± 258 m). Similarly, during 1984 and 1989 transects on the Cooke City area totaled 16.4 km ($\bar{X}$ = 1091 ± 427 m) and 21.1 km during the remaining years ($\bar{X}$ = 1005 ± 405 m). We recorded 124 squirrel sightings, 641 vocalizations, and 300 active middens on the Mt. Washburn study site and 54 sightings, 528 vocalizations, and 201 active middens on the Cooke City study site during the 5 study years. The small number of sightings from the Cooke City site prevented us from estimating annual densities from this measure for this area.

Total distance-to-line frequency distributions for each of the 3 measures did not differ between the Mt. Washburn and Cooke City study sites (Mantel-Haenszel χ^2 for ordinal categories, P = 0.51, 0.61, and 0.35 for active middens, vocalizations, and sightings, respectively). Perpendicular distributions of sightings and active middens peaked in the nearest (<10 m) distance category, although the distribution of sightings more closely resembled a negative exponential and the distribution of middens a negative sigmoidal function. The majority (65% and 78%, respectively, by year and study site) of both these distributions were adequately fit (χ^2 test, $P > 0.10$) by a single-term Fourier function. Distributions of vocalizations peaked in the 2nd (11–20 m) distance category and were characteristically (94%) fit by a 2- or higher-term Fourier function. In 3 (18%) instances we could not achieve an adequate fit by any model.

Relationships among annual density estimates from the 3 measures were varied (Fig. 1). On the Mt. Washburn site, mean sighting and vocalization densities were weakly correlated (r = 0.722), but tended to have overlapping 95% confidence intervals. Only 2 of 9 confidence intervals for the observed estimates (all years, for both the 1984 and inclusive samples) did not contain the line describing perfect correspondence (Fig. 1d). In all but a single instance (Cooke City, 1984), mean midden densities were greater than mean densities of the other 2 measures and were more strongly correlated with sightings than vocalizations (r = 0.981 versus r = 0.831, respectively, for transects 1–57, Mt. Washburn; Fig. 1c). However, in this case, only two of nine 95% confidence intervals for midden and sighting densities included the possibility of perfect correspondence.

CONCLUSIONS

From these results we concluded that densities calculated from active middens were more useful than densities calculated from the other 2 measures for indicating red squirrel abundance. Our conclusion followed from the greater apparent detectability of middens compared to the squirrels themselves, the consistency with which a single-term Fourier function described

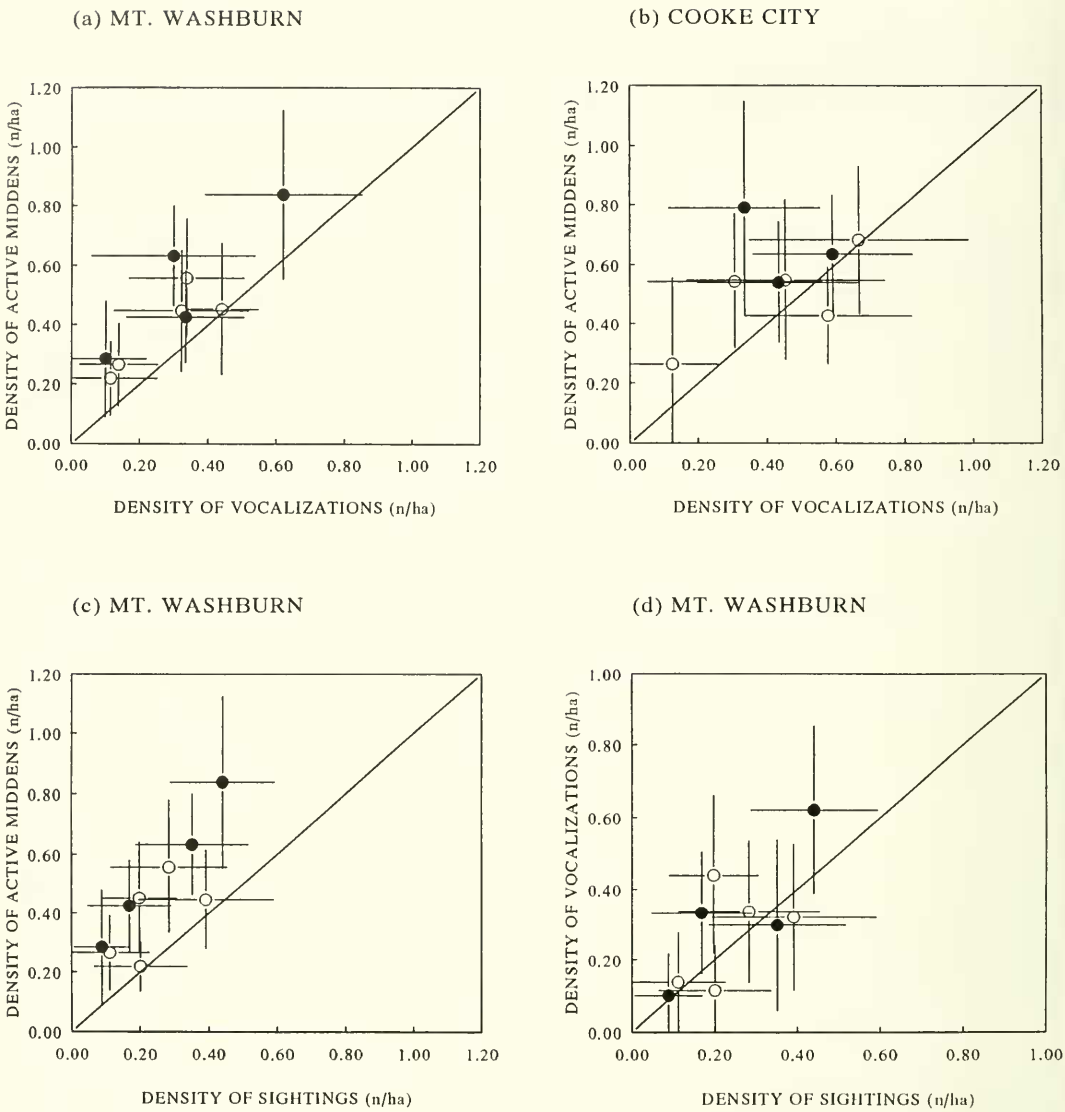

Fig. 1. Relationships between annual estimates of density for active middens compared to vocalizations, (a) for Mt. Washburn and (b) for Cooke City, (c) sightings compared to active middens for Mt. Washburn, and (d) sightings compared to vocalizations, Mt. Washburn, 1984–1987 and 1989. Error bars correspond to 95% confidence intervals, solid circles to results from all transects, and open circles to results from the fewer transects established and first surveyed in 1984. Diagonals represent perfect correspondence between estimates.

the probability detection distribution for middens, and the resulting consistently smaller standard errors for the density estimates. In addition, scatter plots showed that active midden densities tended to be >0 when sighting and vocalization densities were not. By implication, vocalization and especially sighting densities were more likely to underestimate true squirrel densities; i.e., at the same time that active middens clearly indicated the presence of squirrels, sightings and vocalizations could suggest there were none.

Because red squirrel middens are nonmobile, often numerous, relatively easily observed, and typically associated with only one squirrel (Kilham 1954, M. Smith 1968, Wolff and Zasada 1975, Vahle and Patton 1983), they are logical indicators of squirrel abundance. Furthermore, they do not suffer from sampling problems associated with weather, season, and time of day

TABLE 1. Estimated mean (n ha^{-1}) and standard error ($s_{\bar{x}}$) for densities of active middens on the Mt. Washburn and Cooke City study sites, 1984–1987 and 1989, percent coefficient of variations for annual variation 1984–1987, and percent decline in density from 1987 to 1989. Results are given for the transects established and surveyed during 1984 (1–35 and 1–15) and for the larger sample of transects surveyed during all other years, except for 1989, in the Cooke City area (1–57 and 1–21).

	Mt. Washburn				Cooke City			
	Trans. 1–35		Trans. 1–57		Trans. 1–15		Trans. 1–21	
Year	Mean	($s_{\bar{x}}$)	Mean	($s_{\bar{x}}$)	Mean	($s_{\bar{x}}$)	Mean	($s_{\bar{x}}$)
1984	0.447	(0.083)	—		0.428	(0.077)	—	
1985	0.557	(0.110)	0.632	(0.084)	0.682	(0.116)	0.635	(0.095)
1986	0.219	(0.042)	0.426	(0.078)	0.548	(0.126)	0.540	(0.098)
1987	0.453	(0.093)	0.838	(0.143)	0.544	(0.103)	0.790	(0.170)
1989	0.234	(0.062)	0.285	(0.098)	0.262	(0.137)	—	
CV								
1984–1987	35.4		32.6		18.9		19.2	
% decline								
1987–1989	48.3		66.0		51.8		—	

to the same extent as do sightings and vocalizations (cf. C. Smith 1968, Pauls 1978, Ferron et al. 1986). These expectations were corroborated by our analysis. Middens also have a direct tie to management of resources, such as bears, that are of common concern in this zone.

Densities of active middens in our study area averaged between 0.2 and 0.8 ha^{-1}, and on both study sites were lowest during 1989, following the drought and wildfires of 1988 (Table 1). Although annual variation tended to be greater on the Mt. Washburn site compared to the Cooke City site, this difference was not statistically significant (d.f. = 4/4, $F = 1.31$, $P > 0.5$). Both sites exhibited similar annual patterns of variation, including relatively low densities during 1984 and 1986 and a substantial decline in active midden densities between 1987 and 1989.

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LITERATURE CITED

BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monographs 72: 1–202.

FERRON, J., J. P. OUELLET, AND Y. LEMAY. 1986. Spring and summer time budgets and feeding behaviour of the red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology 64: 385–391.

FINLEY, R. B., JR. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. University of Kansas Museum of Natural History Miscellaneous Publications 51: 233–273.

KILHAM, L. 1954. Territorial behaviour of red squirrel. Journal of Mammalogy 35: 252–253.

MATTSON, D. J., AND D. P. REINHART. 1994. Bear use of whitebark pine seeds in North America. Pages 212–220 *in* W. C. Schmidt and F.-K. Holtmeier, compilers, Proceedings—International Workshop on Subalpine Stone Pines and Their Environments: the Status of Our Knowledge. U.S. Forest Service, General Technical Report INT-GTR-309.

PAULS, R. W. 1978. Behavioural strategies relevant to the energy economy of the red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology 56: 1519–1525.

SMITH, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs 38: 31–63.

SMITH, M. C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. Journal of Wildlife Management 32: 305–317.

VAHLE, J. R., AND D. R. PATTON. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. Journal of Forestry 81: 14–15, 22.

WEAVER, T. 1990. Climates of subalpine pine woodlands. Pages 72–79 *in* W. C. Schmidt and K. J. McDonald, compilers, Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-mountain Resource. U.S. Forest Service, General Technical Report INT-270.

WOLFF, J. O., AND J. C. ZASADA. 1975. Red squirrel response to clearcut and shelterwood systems in interior Alaska. U.S. Forest Service, Research Note PNW-255.

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